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Flight behavior of *Luehdorfia japonica* (Lepidoptera, Papilionidae) at the summit area of Mt Egesan, Hiroshima City

1. Hill-topping and round-patrolling of males and their roles in mating and meta-population convergence

Kazuo WATANABE[1)2)]* and Kazuhiko HIRANO[2)]

[1)] Faculty of Integrated Arts and Sciences, Hiroshima University,
Kagamiyama 1-7-1, Higashi-Hiroshima, Hiroshima, 739-8521 Japan
[2)] Graduate School of Biosphere Science, Hiroshima University,
Kagamiyama 1-7-1, Higashi-Hiroshima, Hiroshima, 739-8521 Japan

Abstract We marked 29 individuals (27 ♂ 2 ♀) of *Luehdorfia japonica* (Leech) in 2002 at the summit of Mt Egesan, and analysed their subsequent flight behaviors. The life span at the peak was estimated as 15–17 days. We describe the diurnal changes of the flight tracks and discuss their implications for mating and population convergence. The flight pattern develops in time. After making a short random "wandering flight" in the morning, a flyway of "round-patrolling" with a few preferential staying spots develops. On certain occasions, they manifest a "perching occupation" at a specific staying spot. During the round-patrolling, "spiraling flight" is evoked when encountering another male individual of the same species. And, if the encounter is a virgin female, they copulate. The flight activities of each individual at the peak seem to be individually specific, and generally cover a wider area with aging. During the survey, evidence of peak-to-peak round trips (at least 680 m flight within four hours) was obtained. These behaviors of male individuals produce a widespread coverage of the peak area by a scattered distribution of female-seeking males. This undoubtedly is an effective strategy for lowering the probability of females remaining virgin in the meta-population.

Key words *Luehdorfia*, meta-population, flight behavior, hill-topping, round patrolling, territory, mating, population divergence, population convergence.

Introduction

Many papilionid butterflies manifest "hill-topping" (Shields, 1967) in their flight activities. In *Luehdorfia japonica*, although hill-topping has been well-recognized (Fukuda *et al.*, 1982), and flight behavior of the species has been systematically described in a few monographs (Hirukawa, 1988; Y. Watanabe, 1996; K. Watanabe, 1998), we can seldom find detailed analyses of flight behavior, except for a few data obtained by the mark-recapture method (Matsumoto, 1984, 1994; Natsuaki, 1989, 1996; Natsuaki and Takeuchi, 1999). In a specialized field of Kanazawa City, Central Japan, Matsumoto (1984, 1994) showed population analyses, male patrolling behavior, and several patchy accumulations of individuals along the ridge, and proved eight cases of long-distance flight (526–1,596 m) of marked individuals. In fields of Osaka Prefecture, Natsuaki (1996) and Natsuaki and Takeuchi (1999) proved that males emerged at the bottom of mountains and repeatedly appeared at hill-tops. Also, they observed copulation at hill-tops, suggesting that hill-topping is a kind of mating strategy by males to meet females.

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*Corresponding author. Present address: 5-9-20, Midori, Minamiku, Hiroshima, 734-0005, Japan.
E-mail: kwat@hiroshima-u.ac.jp

To understand the significance of adult flight behavior more precisely, we need to know the totality of behavior at the hill-tops by marking most of the flying individuals, recording their flight activities, and attempting analytical categorization. The problems to be explained are how they meet in order to copulate and how they find their food plant, while at the same time avoiding the danger of population divergence. To accomplish this, it is necessary to select a proper examination field, having an adequate land-structure where the *Luehdorfia*-butterflies can display restricted flight behavior without suffering any interference with other species; this enables us to make strict flight observations and analyses. Mt Egesan of Hiroshima City was considered to satisfy the conditions.

Materials and methods

1. *Luehdorfia japonica* at Mt Egesan

1-1. Characterization of Mt Egesan as a habitat (Fig.1)

A half century ago, the summit area of Mt Egesan (main peak; alt. 582.3 m) was known as a habitat for *Luehdorfia japonica*: however the butterflies were absent or quite rare for 30 years and finally recovered in approximately 1990. Such dynamic changes in a small meta-population seem to occur naturally in many habitats in the Chugoku district (K. Watanabe, 1991). Comparably stable meta-populations still exist, about eight km southeast from here. However, at the same time, an artificial transplantation of the species by anonymous persons is also not completely ruled out. In any case, data in this manuscript indicates that the population is quite small and isolated.

Since 1980, the peak area above the contour of 500 m has been set up as a municipal

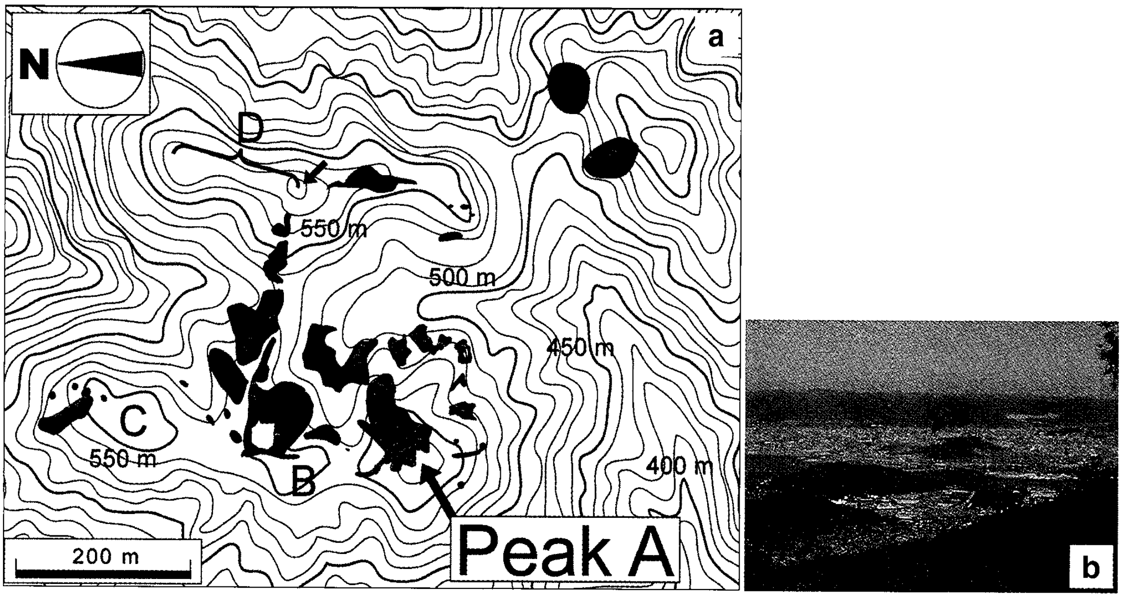

Fig. 1. Mt Egesan as a habitat. (a) Image of distribution area of the food plant, *Asarum hexalobum* (green), and the cumulative oviposition sites (red points) during the last 15 years (1990–2005) by the authors and co-worker, Takeshi Kameyama. The oviposition points move from year to year, and have been quite restricted recently. Peak A is the major survey point. The small arrow at Peak D indicates the recaptured point of marked individual No. 21 on April 19, 2002. (b) Hiroshima City is below Peak A. The arrow indicates the atomic bomb target, 12.4 km northwest from the Peak A.

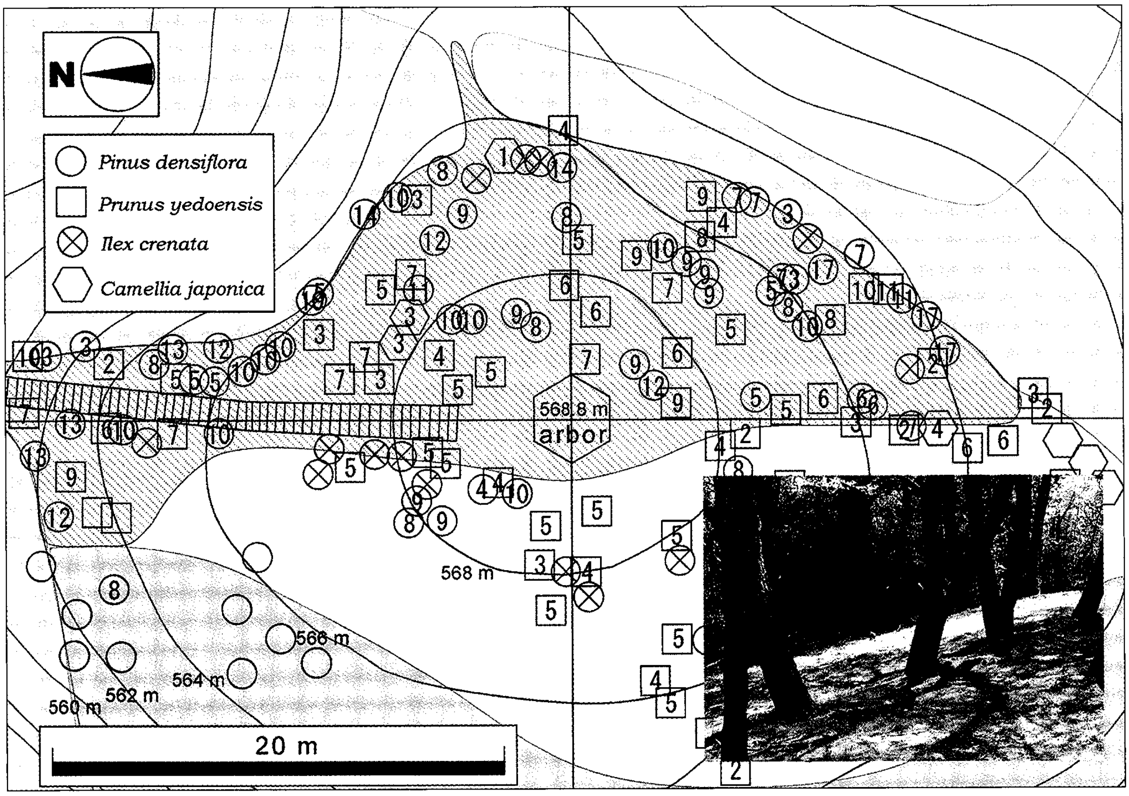

Fig. 2. Cap-like structure of the summit of Peak A with a description of detailed flora. The blue area is bushes of clouded shrubs, where the flying *Luehdorfia japonica* never enter. The yellow area is bright bushes with spotted semi-open spaces where the butterflies occasionally fly about (see Fig. 7, upper left). The green area is a dried grassland, where the butterfly do not like to fly about. The central hexagon is an arbor established by Hiroshima City Office. The ground floor surrounding the arbor (upper than alt. 566 m) is constantly cleaned up by keepers of the municipal park. Numerals in the symbol marks of tree mean the height (m) of the tree. The eastern half of the dome area (hatched) is the main flight area, which is covered with brown-colored fallen leaves of pine trees. The inserted photograph shows the hatched area and the clouded shrubs from the arbor.

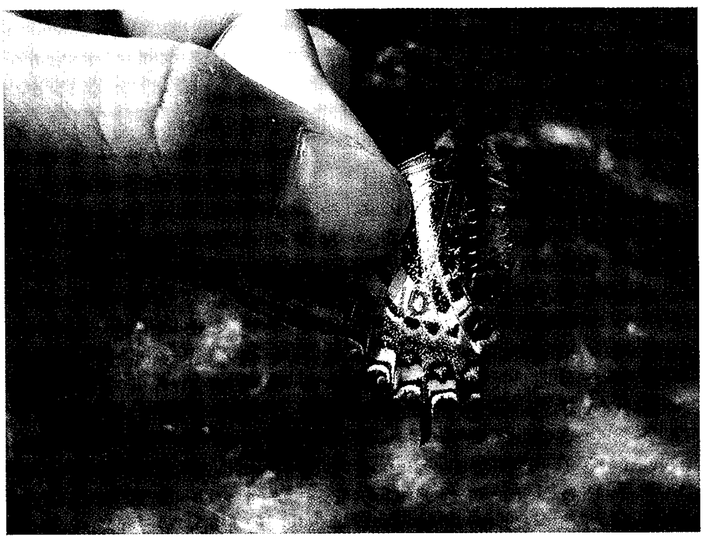

Fig. 3. Markings of *Luehdorfia japonica*.

Egesan park of Hiroshima City, and has experienced continuous artificial manipulation of the flora as a "managed forest". The food plant and laid eggs are distributed mainly in and near the manipulated area (Fig. 1), because the base area, lower than 500 m, is generally covered with untreated thicketed bush, where the food-plant *Asarum* (*Heterotropa*) *hexalobum* F. Maekawa does not propagate well and where adult *Luehdorfia*-butterflies cannot easily invade due to their flight habits. Although there were wide-spread distributions of *Luehdorfia* meta-populations in the vicinities—a few or several kilometers distant from Mt Egesan—until 20 years ago (K. Watanabe *et al.*, 2000), most of the habitat was destroyed during the recent 15 years by development of building-lots and destruction of the circumstances character of the area.

These facts strongly suggest that the collection of butterflies and eggs in these areas would bring about serious damage to the *Luehdorfia* meta-population. Recently, we, along with inhabitants and municipal officers, started a project to conserve and propagate *Luehdorfia japonica* in Egesan Municipal Park (to be published) so that the collection of the butterflies and food plants can be avoided at least until recovery and stable maintenance of a good *Luehdorfia*-population is realized.

1-2. Characterization of the meta-population

The meta-population is a typical peri-Hiroshima Bay population which uses *Asarum hexalobum* as a sole food plant (K. Watanabe, 1991; 1998). Mt Egesan is located on the border of the two sub-metapopulations, which differ in their emerging periods; one is eastern late-emerging which seems to manifest five to seven days later emergence every spring, and the other is northwestern early-emerging (Hashimoto, 1991; K. Watanabe, 1998).

By analysing base sequences of *ca* 800 nucleotides of the mitochondrial *ND5* genes of 10 Mt Egesan individuals (data not shown), the population manifested typical "Hiroshima-Tottori type", which showed a specific SNP (single nucleotide polymorphism) at the base of 107th, that is, a co-existence of 107-A type and 107-G type in the same meta-population (Hirowatari and Watanabe, 2000).

2. Detailed description of the survey point (Peak A)

The summit of Peak A (alt. 568.8 m) was a cap-like open land (*ca* 50 m $\times$ 30 m) with flat managed ground (Fig. 2). The western half was open grass land and the eastern half was a sparse woody area of pine trees (*Pinus densiflora*) and planted *Prunus yedoensis*, with a hexagonal arbor in the center (Fig. 2). The situation made it possible to watch and record multiple flying individuals at the same time. In this season there were no flying butterflies in the area other than *Luehdorfia japonica*.

In the summer of 2004, the peak area was completely destroyed at a plane of alt. 560 m-contour by public construction of a radio wave tower (121.03 m) with an adjacent four-story building for digital-TV broadcasting.

3. Marking of individuals and following-up of their flight activities

Markings were made on the ventral surfaces of hind-right wings (Fig. 3) using color magic pens (oil-type, Mackie-Gokuboso, Zebra Co.). We tried to mark all the individuals that visited Peak A and adjacent peaks during the survey periods (April 3 to 26, in 2002). Although a few individuals at first escaped our capture and remained unmarked, in many cases they revisited the peak and were marked. As almost all the individuals observed at the summit had markings (Figs 4, 5), the escaped individuals seemed to have been rare.

The visiting times and their flight tracks were all recorded and traced on a map based on

Fig. 2. All the data described was recorded by the junior author (KH), with the occasional assistance of the senior author (KW). Identification of markings was made using two methods. The first was direct observation of the resting individuals using naked eyes and field glasses (Nikon: Micron 7×15 CF). The second was confirmation of markings by capturing the flying butterflies with a net, and after recording the markings, the butterflies were released. As we could not distinguish any recognizable effect on flight behavior as a result of repeated capturing and releasing, we concluded that such effects were negligible.

Results and discussion

1. Flight activity and life span at the peak

1-1. Flight activities

We marked 29 individuals (27♂2♀) at the summit area (Peaks A, B, C) in 2002 (Fig. 4). The fact that 93% (27/29) of the flying individuals were males indicates that the hill-topping is performed mainly by males, or at least that it was in that year.

Fig. 5a clearly shows that the butterflies immediately stop flying and disappear in cloudy conditions. The regularity is quite impressive, as if the flight activities are rigidly restricted not only by brightness alone but also by another unknown determining factor, such as polarized light patterns.

1-2. Timing of emergence and life spans

After the first emergence (April 1) at the peak, four fresh unmarked individuals were captured as late as April 19 (more than half a month later) (Fig. 4). The four might be heralds of a late emerging population as previously suggested (Hashimoto, 1991; K. Watanabe, 1998). However, we still cannot determine whether or not there are two such populations with different genetic backgrounds. It is in any case interesting that the Mt Egesan population displays a long duration of the adult emergence period, even though Mt Egesan, in southern Hiroshima Prefecture, has a temperate climate and is not a snowy province where the differential melting of drifted snow would expand the duration of adult emergence.

In the cases of Nos 9 and 10, they were observed for at least 15 days at the peak (Figs 4, 5b). Their wing conditions were completely fresh on the first day and heavily stained on the last day. And the flight activity on the last day looked quite attenuated, indicating that the life span of the individuals in the longest case was around 15–17 days. This was consistent with the data of Matsumoto (1984) in Kanazawa City. Additional data recorded in 2003 and 2004 also confirm the fact (Hirano *et al.*, 2006).

2. Are the flight behaviors at the summit individually specific?

From 20 individuals marked from April 3 to 13, eight individuals were observed at the peak, for periods exceeding five days (Figs 4, 5). It is remarkable that a considerable number of early-emerging individuals stay around the peak area. On the other hand, individuals marked on April 19 were not observed for such a long time (Fig. 4). The question arises whether the late-emerging individuals have a tendency for stronger migratory activity. However, at the same time, seasonal changes in temperatures and daylight conditions during these two weeks may not be negligible and should be taken into account.

The data showed that some individuals repeatedly appeared at the peak; on the other hand, other individuals appeared only once or a few times, indicating that flight habits at the peak are individually specific, and that habits might change with aging (Fig. 5b). For example,

Day/April	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
WTHR	F	F	F	F	F	R	C	F|C	C/F	C/F	C/R	F	F	F	R	R	R/C	C	F	C	R	C	R	R	C|F	F|C	C|F	C|F	C	C
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Fig. 4. Mark-recapturing at the summit area. The days of survey are expressed at the top of the figure by large gothic-italic letters in the green box. Markings (No.) of the left-side ordinate are marked individuals (1–29). Fillings with blue color (1–27) represent males, and fillings with orange color (28–29) are females. Peaks, firstly marked and/or recaptured, are distinguished by color as follows. Pink: Peak A, Yellow: Peak B, Green: Peak C, Blue: Peak D. No. 21 individual at the 19th day (Violet) means it was recaptured at Peak A and Peak D on the same day. WTHR: weather, F: fine, C: cloudy, R: rainy, F | C: fine and later cloudy, F/C: fine and occasionally cloudy. Conditions of butterfly wings are expressed as follows. frs: fresh, md: medium stained, stn: extremely stained.
Marking and recapturing were mainly made at Peak A (23 males and 1 female). Peak B is located on the route approaching Peak A. On the days of plural investigators, they moved around the peaks, but K. Hirano always stayed at Peak A. There is a strong possibility that the 3 individuals (3/6) marked on April 3 include the individuals eye-witnessed on April 1. At the marking of No. 9, half of his hind-right wing, the usual marking area, was already lost, suggesting that the individual was No. 2 or No. 5 individual marked on April 3. In this case, marking (or re-marking) was made on the remaining hind-left wing. Individuals with heavily damaged (or lost) proximal halves of hind-right wings at the first capturing (Nos 9, 18, 21), are identified with parentheses in the figure.

although individual No. 4 (flying there for 11 days) had a tendency of occasional appearance at a young age, he changed his habit to stay for a long time at the peak in his older age. No. 9 stayed at the peak on the afternoon of April 5, and after a long (13 days) absence, again appeared there on April 19. No. 11 showed a tendency of appearing there repeatedly with a certain absent period (more than 20 min) in the same day. No. 14 appeared in the afternoon at a younger age, but later in the morning (Fig. 5b).

When we compare the flight track of No. 4 and No. 14 in Figs 6a, b, we can recognize that No. 4 tends to fly out over wider ranges of eastern clouded bushes from 11: 00–13: 00 (see green arrows in “ALL” of Fig. 6a). As for the flight habit of No. 14, we could not recognize such a tendency (Fig. 6b), suggesting that the flight behaviors are individually specific.

As human visual range is restricted to about 4 m in height and 90° in width, strict implication of the absence of butterflies remains a subject of discussion. One of the points involves how far they are flying from the peak. We will reply, in part, to the question in Section 4.

3. Daily progression of flight activities at the peak

Out of many flight-track data, we show examples of No. 4 in Fig. 6a, and No. 14 in Fig. 6b.

3-1. Acquisition of flight-track consistency

Many males finish their daily flight activity at the hill-top of Peak A and take an overnight rest there on the leaves of pine trees. One author (KW) during these 15 years at Peak A has witnessed several cases in which inert males have fallen as a result of weak flight from pine trees to the ground before their start of daily activities at around 8: 30 am (K. Watanabe, 1998).

After random preparative flights for a short time, the butterflies start to manifest a typical flight pattern, called “wandering flight” (Y. Watanabe, 1996; K. Watanabe, 1998), in which they fly at a height of about 20–70 cm from the floor surface as if they are wandering around. The flat floor consisted of deep yellow-brown dead leaves of pine trees showing a dappled color (“Kanokomadara” in Japanese) as a result of the sunlight through the crown leaves.

The butterflies repeatedly rest (5–10 seconds) on the ground followed by wandering flight of (10–30 seconds) for about 15 min. Eventually, the butterflies tend to come along to sunlit areas in otherwise shady areas. To visit a few preferential and specialized spots successively means the flight path becomes straight. The consistent flight tracks seem to be produced by “looking” at the brightness pattern in front and by joining in a line a few bright spots. In preparative flight, the butterflies look as if they are oriented only to the ground surface, but in straight flight they have to watch in front using their compound eyes (Arikawa, 2001).

From the whole day flight-track data (Figs 6a, b), we can recognize the flight track is never random but frequently has a consistent flight route. And, the flight routes of No. 4 and No. 14 were well-overlapped. Further, we can recognize that there were a few preferential accumulating spots which corresponded to the brighter areas (1–2 m in diameter) in the course of the flight track.

3-2. Round patrolling with resting points

With time, flight activities became more active and flight areas wider, and the butterflies occasionally flew away from the observation area. Importantly, in due time, they came back again to the peak (homing-in) (Figs 6a, b). This resulted in them traveling in a circular loop.

(a)

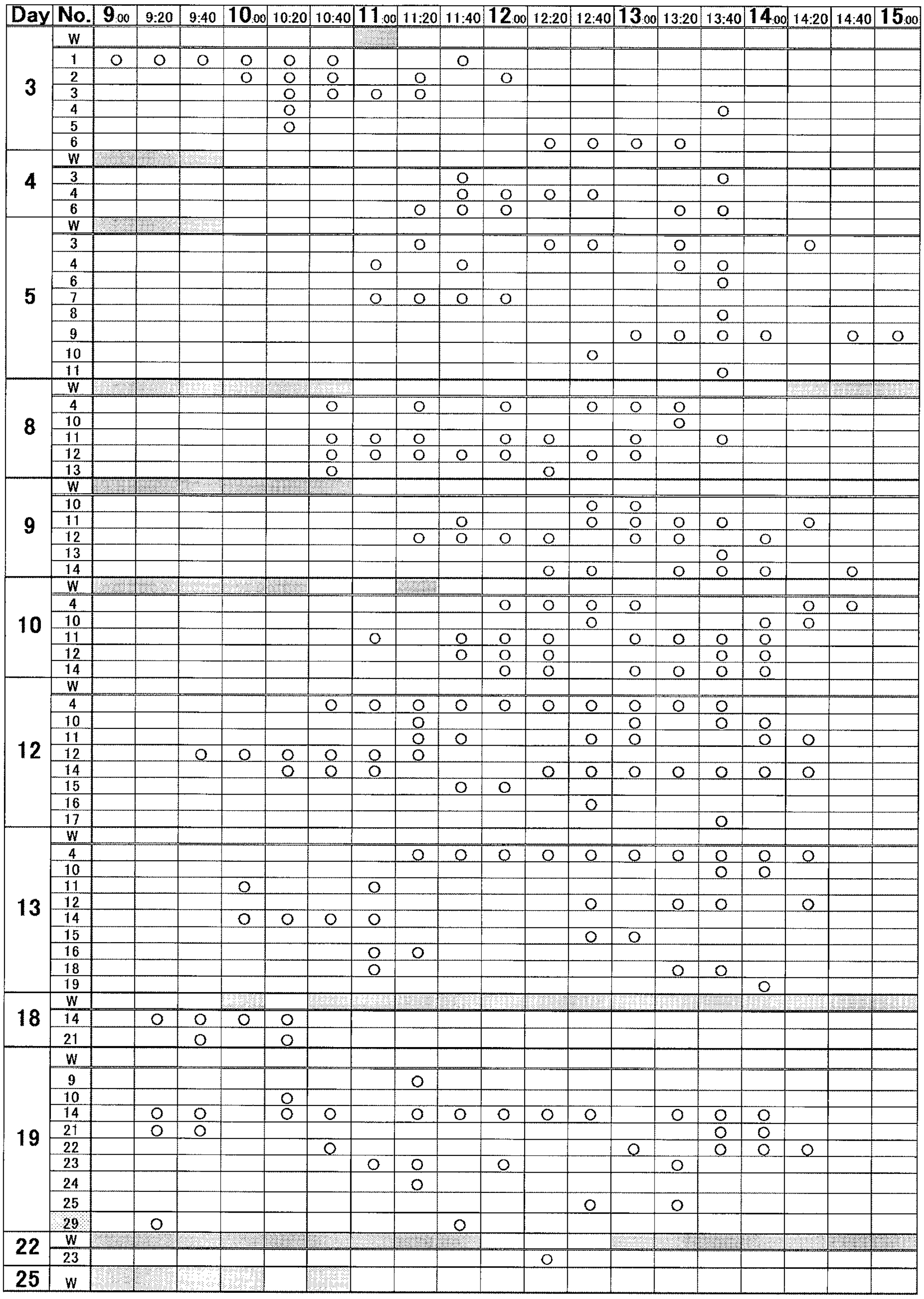

Fig. 5. Detailed timing of the emergence of the marked individuals at Peak A. (a) Diurnal changes summarized for all survey days. (b) The data of (a) was rewritten for each individual (Nos 1–29). The top line expresses the time of appearance of the butterflies at Peak A. 9: 00 means from 9 o'clock to 9 o'clock 19 minutes 59 seconds, and 9: 20 means from 9 o'clock 20 minutes to 9 o'clock 39 minutes 59 seconds. W: weather (conditions of sunlight). When the sunlight was shaded by clouds, the boxes are shadowed. Day: Survey days in April. No.: Identification number of marked individuals.

(b)

No.	Day	9:00	9:20	9:40	10:00	10:20	10:40	11:00	11:20	11:40	12:00	12:20	12:40	13:00	13:20	13:40	14:00	14:20	14:40	15:00
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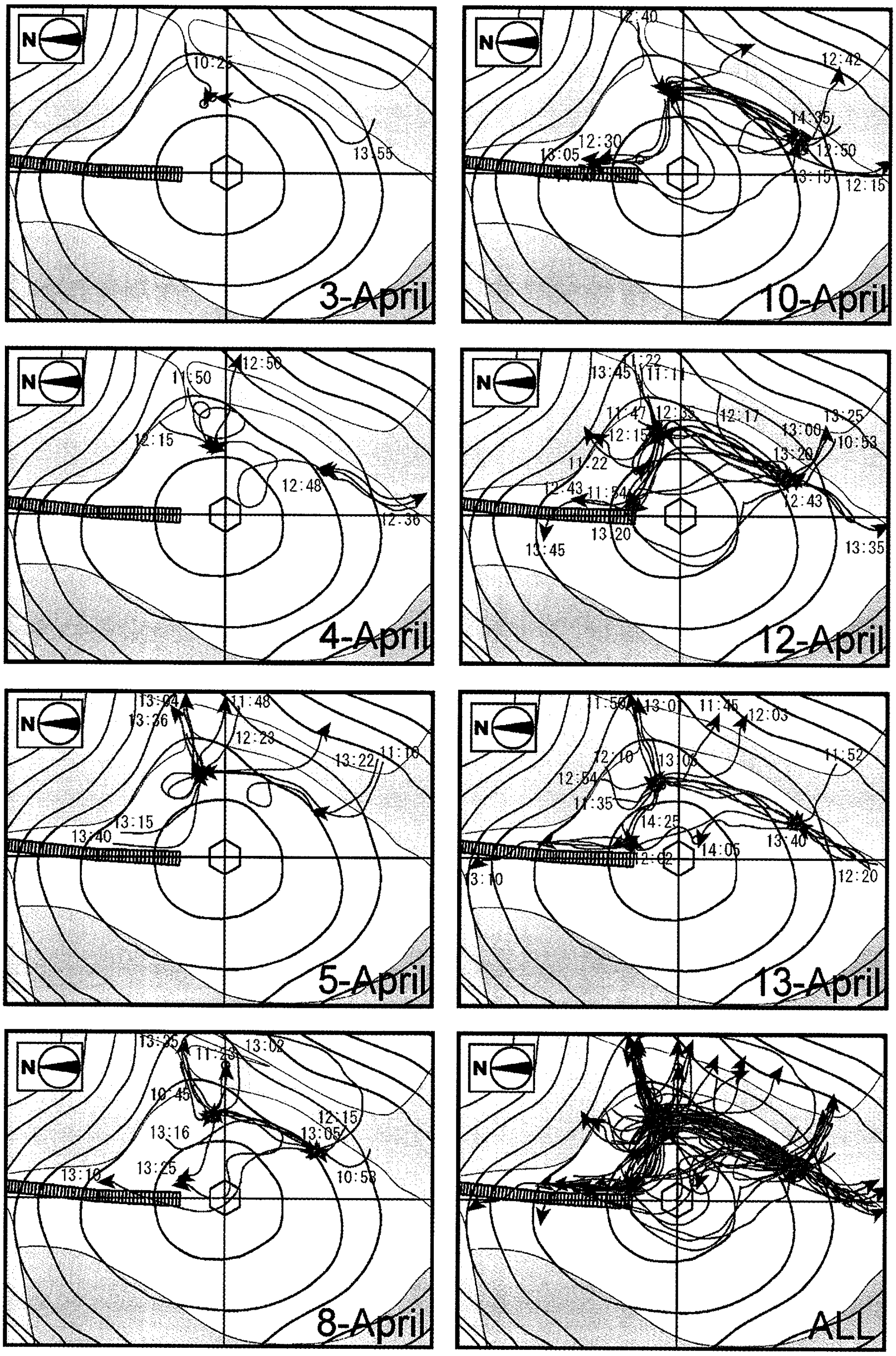
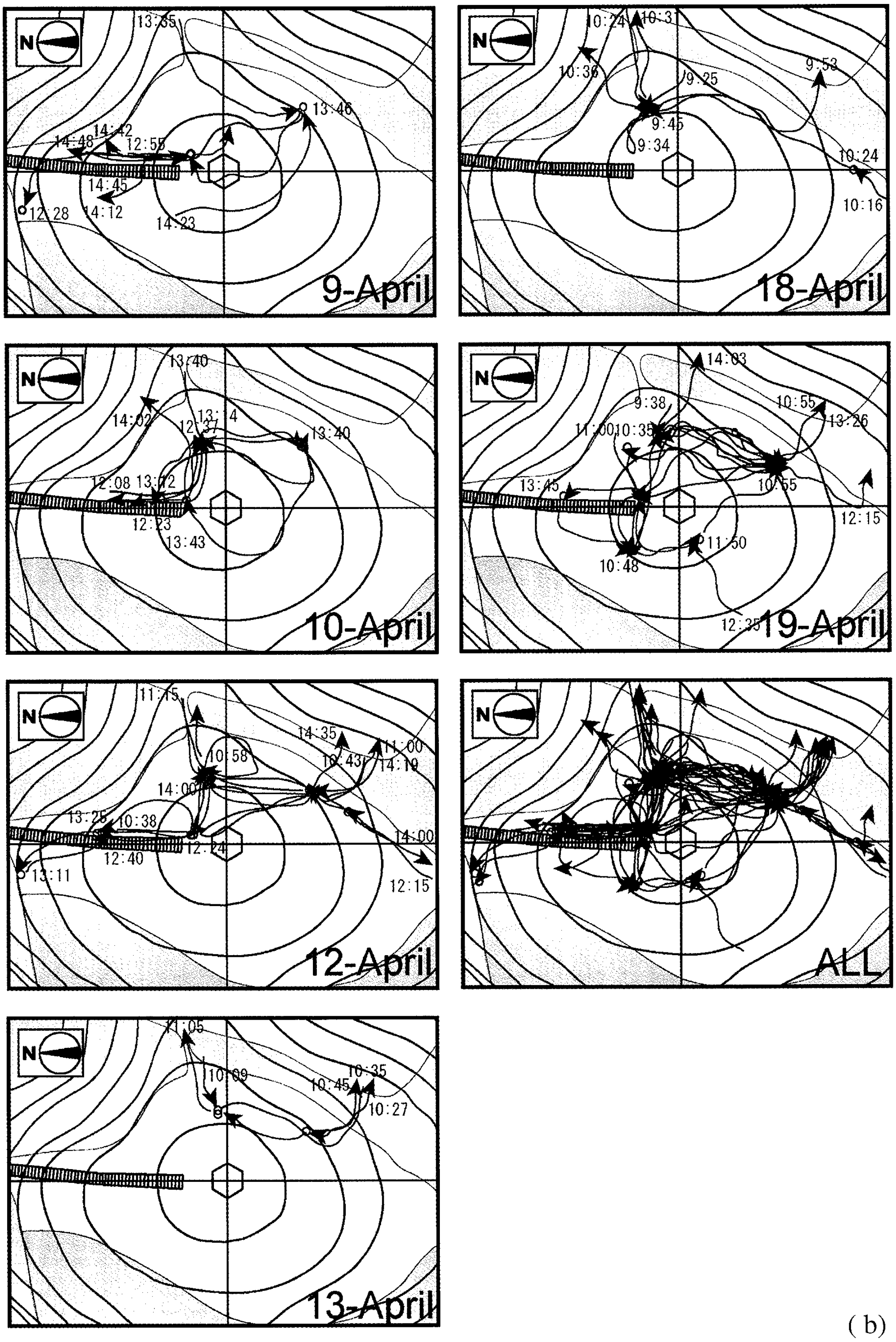
29	19		○							○										

In the looping observed in the case of No. 14 on 11 o'clock, April 12, the butterfly flew away from a point (over bushes composed of *Eurya-Camellia-Rhododendron* with a height of *ca* 2.5 m; right photograph in Fig. 7), traveled in a circle along a route (about 50 m), and finally came back from another route (the northeastern small path; left photograph in Fig. 7). In the case, the butterfly spent certain times at six precise resting points; three were bright areas at the hill-top, and the other three were bright areas along the eastern slanting surface over the bushes (Fig. 7). At these points, the butterfly spent about 10 seconds–3 minutes, displaying a few repeated rests and flights (*ca* 2–20 seconds rest and *ca* 3–20 sec-



(a)

Fig. 6. Detailed flight-tracks of two examples (No. 4 and No. 14) in each day and the cumulative sum of them (ALL). (a) The case of individual No. 4. (b) The case of individual No. 14. Blue letters and lines were flight tracks of 9: 00–10: 59, green were 11: 00–12: 59, and red were 13: 00–14: 59.



(b)

onds flight). As a result, it took a long time (*ca* 15 min) to complete a round trip in this case. We emphasize that, without stopping, it takes only about 20 seconds to complete the round flight on this route. Preliminarily, we measured the time of temporal absence (from flying out to returning) in individuals at the Peak A (No. 4 and No. 14) from field notes (Table 1). The data showed that, from flying out to returning, about 5–20 minutes were the most frequent case. The facts strongly suggested that the butterflies seemed to use similar

Table 1. Measurements of time of absence at the Peak A (from flying-out to coming-back) in individuals No. 4 and No. 14 (preliminary calculation from field note).

Time of absence (minutes)	Frequency
0–5	1
5–20	11
20–30	5
30–40	2
40–	5

flight routes with similar resting points. We call this "round patrolling with resting points".

The significance of round patrolling by males is considered to be related to raising the chance to encounter virgin females. In addition, we emphasize that making a loop has a great adaptive significance to avoid population divergence, which is the most dangerous situation for meta-population maintenance.

3-3. Perching occupation with repeated circular flights

In an earlier report (K. Watanabe, 1998), the author described a specialized male behavior at Peak A in 1993. We call it "perching occupation with repeated circular flights" (Fig. 8). The male looked to be highly excited, and manifested perching and repeated the circular flights, as if the male was "scrambling" toward an unknown entity. As the previous description was written in Japanese, here we give a brief re-description in English.

"On April 19, 1993, the author (KW) arrived at Peak A at 12: 30. A few males were flying there, and in due time the peak became silent. Several minutes later, the author was aware that a male perched on a dried eulalian leaf (height of *ca* 1 m) (Fig. 8a and blue point in Fig. 8b), where he was making the repeated circular flights as follows. The open space was *ca* 5 m in diameter surrounded by four pine trees, where the butterfly repeatedly undertook quick counterclockwise circular flight (*ca* 4-second flight with 10–20 second rest) with a flight diameter of *ca* 4 m and a flight height of 1–2 m (blue circle in Fig. 8b). This meant 2–4 repeats/min of the circular flight. It continued the behavior there for at least 10 min, while the author could not find any invading insects.

At 13: 30, a virgin female appeared from the north and stayed on the trunk of a cherry tree (red point in Fig. 8b, 13 m northwest from the repeated circular flight site), and she opened her wings 180°. After 30 seconds there, she flew directly toward the circular flight area of the male (red line) and stayed on the pine leaf at a height of 2 m with her wings folded, and there was ca 50 cm distance from the male's flight track (red circle in Fig. 8b).

Surprisingly, the male did not suddenly copulate with the accessible female, but waited a further *ca* 3 min. This interval felt quite long for the watcher, since, in general, male individuals suddenly copulated, when encountering virgin females. During the interval, the male displayed 8 further ordinary circular flights. In this situation, the distance between the resting points of the male and the female was about 5 m. Furthermore, quite importantly, the female with the folded wings opened them 45–160° for about one second, just when the circular flying male approached *ca* 100–50 cm to the female, as if she was tempting him. After repeating 8 such flights, the male unexpectedly and suddenly collided against the female, and instantaneously the two copulated.

It is likely that in *Luehdorfia japonica*, the repeated circular flights do not have such importance for defence of territory and attachment of the female as in the case of nymphalids, but

may have a role in allowing the accessing female to find the male by displaying his moving tiger-striped color pattern (Hidaka and Yamashita, 1975; Hidaka, 1998) during his repeated circular flights.

In this case, another male individual occupied another base point for his repeated circular flight (Point B in Fig. 8b) at the same time, which was at the tip of a shoot of *Rhododendron reticulatum*, as if these two males occupied two adjacent territories which were mutually exclusive and never overlapped. The two points were 20 m apart and out of mutual visual range, and we could not observe any apparent interaction between the two males."

We would like to characterise the behavior as a more advanced physiological state than resting at specific sites in the course of round patrolling. However, we have to confess that, in spite of our intensive observations of more than 10 years, we have not been able to observe such typical "repeated circular flights" again, suggesting the physiological conditions to evoke the behaviour are quite restricted. A lapse of time, a rise in temperature, the number of males nearby, the presence of preferential staying structure with proper light conditions, among other factors, could evoke the behavior.

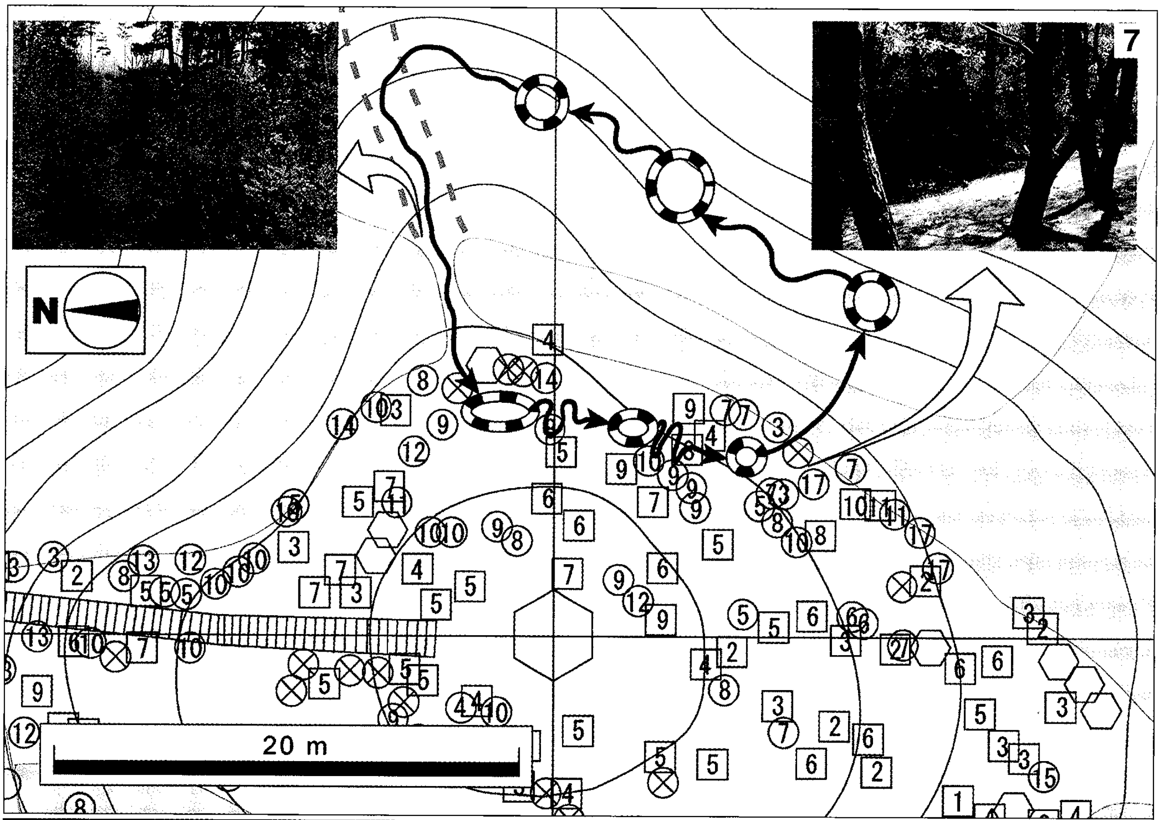
The behavior and next spiraling flight seemed to be similar to "territorial behavior" which had been discussed as mating behavior in nymphalids (Baker, 1972; Kemp, 2001; Mi. Watanabe, 2002) and lycaenids (Cordero and Soberon, 1990; Takeuchi and Imafuku, 2005). However, as our observations were considered to be specific for *Luehdorfia japonica* in many aspects, we avoid here making generalizations, but only describe the facts. Designed analytical observations and experiments are required based on preceding discussions (Scott, 1986; Mi. Watanabe, 1988; Hidaka, 1998; Kemp and Wiklund, 2001; Prokopy and Roitberg, 2001; Honda, 2005; Ma. Watanabe, 2005).

3-4. Spiraling flights and horizontal chasing evoked by encounters with other males

When two or three male individuals meet, they immediately begin spiraling flight behavior. In a similar flight pattern, Sibatani (1989) used the term "co-rotating flight", and Kemp and Wiklund (2001) and Takeuchi and Imafuku (2005) used "circling flight". Although the flight patterns are considered to share many elementary processes, we cannot confidently compare them, since basic processes are still not fully analysed and the phenomena should be, more or less, species-specific.

In *Luehdorfia japonica*, after the spiraling flights, one of two behaviors occurs. One is a horizontal chase after 1–3 seconds of spiraling (Kemp and Wiklund, 2001), and the other is separation and independent flight. The ratio of the two seems to be strongly dependent on environmental conditions. Similarly, when both individuals flew away by horizontal chasing, the outcome was one of two. In the first case, the original occupier came back within a few seconds. In the second case, both individuals flew away from our visible range, and importantly, there was a possibility that the chaser was not always the original occupier; there could have been cases in which the chaser was the invader. After long absences for several minutes, an individual came back to the point and stayed there because the point seems to have certain advantages. We cannot now determine whether the individual was the original occupier or the invader.

The behavior features an adaptive implication for female-seeking males to ensure a scattered distribution by avoiding excessive male accumulation at the same point. If the invader was a virgin female, they attained copulation.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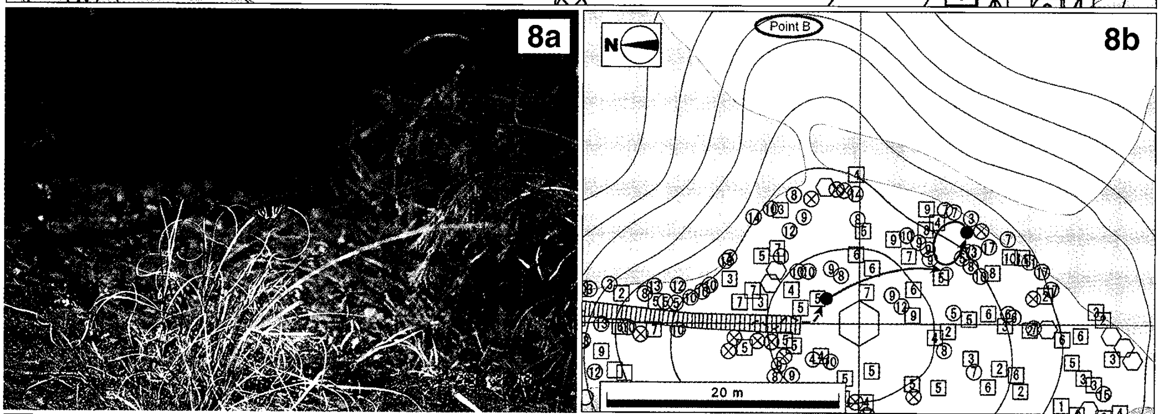
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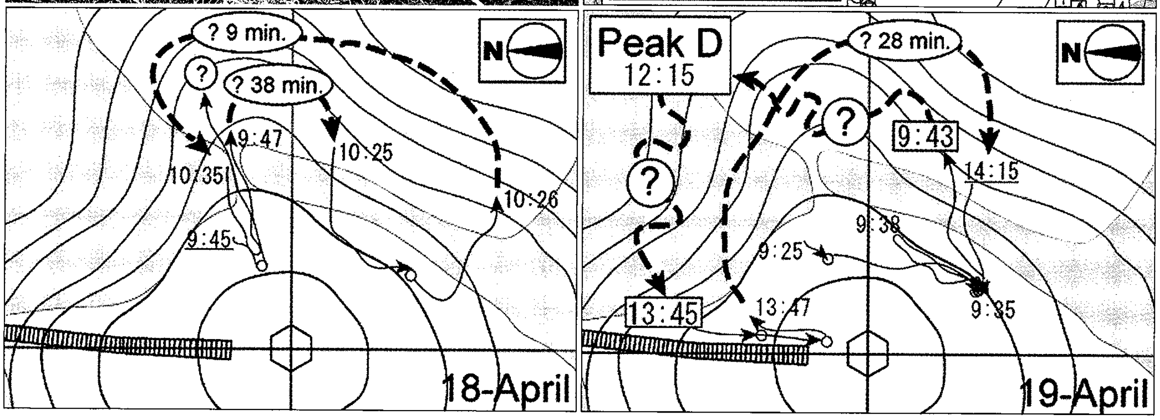
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18-April
Peak D
12:15
? 28 min.
?
9:43
14:15
9:38
9:25
13:45
13:47
9:35
19-April

9a 9b

3-5. Temporal changes of the flight area

Accumulation of the flight track data revealed that the tracks manifested a tendency toward a consistent temporal change, as they were restricted by the sunlight conditions and physiological states of the butterflies themselves.

From morning to afternoon, we can recognize that the main flight area changes from east to north (Figs 6a, b), mainly depending on the changes in shade and daylight angles on the ground. Next, we can point out that the flight area has a tendency to become wider from morning to afternoon.

Generally, the flight area became wider as the butterflies grew older (Figs 6a, b). This situation was the same in the two marked individuals (Nos 4 and 14). Whether the consistency is dependent on a certain physiological memory of the flight experience is an interesting future problem.

4. Evidence of peak-to-peak translocation on the same day

An individual (No. 21), which was marked on April 18 at Peak A and displayed a flight activity from 9: 45–10: 35, manifested a surprising flight the next day. On April 19, he appeared at Peak A at 9: 25. And, after certain flight activity, he flew away from Peak A at 9: 43 (assured by KH) and was recaptured at Peak D (alt. 582.3 m, small arrow in Fig. 1), which is 340 m distant from Peak A, at 12: 15 by our co-worker, T. Kameyama. Further, surprisingly, the individual came back again to Peak A at 13: 45 (assured by KH) (Fig. 9), indicating the individual round-traveled actually more than 680 m within the four hours. This fact strongly suggests that butterflies travel such long distances frequently and that the mark-recapturing method is useful to detect it.

General discussion and conclusions

The adults of *Luehdorfia japonica* actively fly in mountainous open land, in spite of their small population size, short emergence period, and restricted food-plant preference. Without a doubt, the most dangerous problem for survival of the meta-population in such species is population divergence. Accordingly, the butterflies have to sustain specific flight mechanisms to satisfy feeding and mating requirements. Displays of “hill-topping” and “round-patrolling” are understood as mechanisms.

The diurnal periodicities in the flight behaviors of males at the hill-top are understood as a step-wise upward regulation of an intrinsic physiological state (Table 2), coupled with the lapse of time, rise of temperature, and number of males at the summit area; the goal is to acquire a virgin female. Mutual exclusion of male individuals by spiraling flight, under the condition of loose territorial behavior in round patrolling, produces widespread coverage of

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Fig. 7. Round patrolling with spotty staying points on April 12 (No. 14) at 11: 00, as an example. The flying-away point is shown by the inserted right photograph, and the return point is shown by the inserted left photograph. In the center of the right photograph, we can see a yellow spot of flying *Luehdorfia*.

Fig. 8. Perching occupation with repeated circular flights on April 19, 1993 (see K. Watanabe, 1998). (a) A male with the pose of “starting” for the circular flight on a dried eulalian leaf. (b) Drawing of the male flight track (blue circular line) and access route of a virgin female (red lines) in the case.

Fig. 9. Flight tracks of No. 21 on April 18 (a), and April 19 (b).

Table 2. Progressive changes of flight behaviors in a day.

(Phase 1) Wandering flight with a few preferential accumulation spot
(Phase 2) Establishment of flight path by connecting the accumulating spots
(Phase 3) Round-patrolling with resting points
(Phase 4) Perching occupation with repeated circular flight

the summit area by numerous female-waiting males. In fact, the summit area is one of the important places for copulation of *Luehdorfia japonica* (Natsuaki, 1996; K. Watanabe, 1998). Copulation attained in front of the authors at Peak A was counted at least 24 times during these 15 years.

With the goal of lowering the probability of leaving virgin females in the meta-population, this would be an effective strategy for *Luehdorfia japonica*, which must survive in the complicated mountainous habitat of Japan with its mosaic of thickets and open lands. Flight behaviors of females, especially the differences, if present, between virgin females and post-copulated females, are an interesting future problem.

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摘　　要

ギフチョウの飛翔行動 (1) (渡辺一雄・平野和比古)

2002年4月1日から26日までのべ14日間, 広島市絵下山山塊の無名峰 (568.8 m) において, ここに飛来した全てのギフチョウ成虫29個体 (27雄2雌) をマーキングし, 雄個体の山頂への出現およびその飛跡を時間を追って地図上に記入し, 飛翔トラックを解析し, 山頂集合性, 日周変動, エイジング変動を記録した. ギフチョウの雄は約2週間の寿命を持ち, 山頂固執性が実証されると共に, 山頂固執性が顕著に判別できる個体とあまり判別できない個体の存在が示唆された. 行動範囲は1日のうちでは午前から午後にかけて, また若年期より老年期ほど広くなる傾向が認められた.

飛跡追跡により, ギフチョウの飛翔ルートは個体ごとに, また個体間でも, ある程度整合性の高い共通の飛翔ルートを持つことが示唆された. また, 一定の巡回飛翔 (round-patrolling) を行ってもとの山頂に戻ってくる性質があること, また特定の占有位置確保 (perching) の上, あたかも“スクランブル”するかのように一定の時間間隔で一定の空間を, 数秒間の円形トラックの哨戒的飛翔 (repeated circular flight) する場合があることが認められた. 2頭以上の雄個体が遭遇すると, らせん飛翔 (spiraling flight) を行う. これにより複数の雄個体の集積を避け, 山頂部の広い範囲を雄の数個体がspacing-out しつつカ

バーしあって未交尾雌の飛来を待つ体制をとっていると考えられた. 遭遇個体が未交尾雌の場合, ここで交尾が成立する. 以上の飛翔行動は, 個体の散逸を防止しつつ, 同時にメタ個体群内部に未交尾メスを残さない優れた行動戦略と解釈された.

マーク個体のうちの1個体は, 約340 m離れた峰と峰の間を約4時間を要して往復した. 少なくとも直線距離で680 m以上の飛翔行動を4時間以内に行って,もとのピーク（地点）に戻ってきたことになる. すなわち, ギフチョウは周辺のいくつかの峰を巡回する場合があると推測された. これらの行動は, 先述の巡回飛翔の拡大という観点から考察された.

なお, 近年, この周辺地域のギフチョウの衰亡が顕著であり当地の個体群はすでに相当度に孤立している証拠がある. これに加えて, この調査点の山頂部は, 2004年6月, デジタルテレビ塔およびテレビ局舎建設に伴って完全に破壊された. 筆者らの一人, 渡辺は, 広島のテレビ局5社, 広島市, 施工業者からなる「絵下山公園デジタルテレビ塔建設事業にかかる環境の保全に関する協議会」の会長として, 広島市および工事関係者の協力の下に公園全域のギフチョウ生息環境の保全および生息個体数の増幅とその保持を目指した最善の努力を行っている. また同時にこの山塊全域の調査を続行している. 充分に個体群の保持が可能な状況が現出するまで, 当分の間, 採集者は絵下山公園内におけるギフチョウと食草の採取を控えるよう強く期待する.

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